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The Phyllodes of Oxypolis filiformis, a Swamp Xerophyte*

BY ROSINA J. RENNERT

A large number of species of higher plants which live in ponds, marshes and other extremely moist habitats present structural characters of a xerophytic nature which have been most difficult of interpretation. A special study of the phyllodes of *Oxypolis filiformis* † was undertaken by the author in the hope that some additional light might be thrown on the subject. This work was carried on in the New York Botanical Garden under the direction of Dr. D. T. MacDougal, to whom I am indebted for valuable advice and fruitful suggestions.

Oxypolis filiformis is an umbellifer which grows in swamps and along the borders of ponds in the southeastern United States, as far north as Delaware. The leaves exhibit curious modifications by which they depart widely from the uniformly broad or widely dissected umbelliferous type, being reduced to stiff grayish-green awl-shaped phyllodes, which have a structure as if made up of a number of sections of varying lengths, the joints being distinctly noticeable and marking the position of peculiar septa in the interior tissues. This habit of the leaves gives the plant a rush-like appearance, an effect which is heightened by the small size of the cauline, and the strong development of the basal phyllodes. The entire phyllode is flattened along one side. A minute pit is to be observed externally to every septum, occurring in the middle ot the slightly flattened surface.

Briquet ‡ has given a detailed account of the results of his examination of this plant with respect to the anatomy of the phyllodes. He describes the epidermis as a single layer of cells with curved outer walls protected by a thickened outer membrane and a folded cuticle. The stomata were noted as either flush with the surface, or sunken slightly below, being about 48 to 54 μ in length. Directly underneath the epidermis is a hypoderm composed of small sclerotic cells with a small lumen. The hypoderm is one to three layers in thickness, and is interrupted only underneath the stomata. The chlorophyl-bearing tissue consists of three to six layers of cells, the outer ones of which are palisaded. The innermost layers are more loosely arranged. Internal to the chlorophyl-bearing cells is a cylinder of four or five layers of large thin-walled cells, designated as endoderm by Briquet. The fibro-vascular bundles are situated in this tissue. The pericycle comes into contact with the chlorophyl-bearing tissue in places, however. The axial portions of the phyllodes were found to consist of thin-walled stellate elements which are in contact at the tips of the rays. The septa were found to be composed of sclerotic cells with numerous branching canals extending radially through the walls. The fibro-vascular bundles are unbranched in the intervals but break up at the septa and form a mesh of anastomosing branches, which however do not traverse the septa radially to any great distance.

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* Read before the Botanical Society of America, by invitation, at Pittsburg, Pa., July 1, 1902.

† OXYPOLIS FILIFORMIS (Walt.) Britton. *Tiedemannia teretifolia* (Muhl.) DC.

‡ Briquet, J. Etude de la feuille du *Tiedmannia teretifolia* DC. Bull. Herb Boiss. 5 : 461-465. 1897.

Briquet explains the seemingly anomalous possession of transpiration-hindering hypoderm by this marsh plant by the fact that it is subject to two extremes of conditions. The mechanical advantages from the cylindrical form of the phyllodes, and the aërating capacity of the stellate tissue would be of advantage during the early spring season, when the plant is more or less submerged. The shape of the leaf would present a reduced surface and the hypoderm would check transpiration during the mid-summer season after the waters have subsided.

My own examination of this plant and the results of the experimental tests made with it have revealed some structural features not mentioned by Briquet, and lead to a somewhat different interpretation of its adaptative features.

Some plants brought from Georgia and Florida in 1901 and 1902 were grown in the greenhouse under various conditions as described below. The septa in the phyllodes of these specimens were found to consist chiefly of small thin-walled cells containing chlorophyl, and resembling the elements of the other chlorophyl-bearing tissue, with only an occasional thick-walled sclerotic cell. The endoderm was found to be continued on the surfaces of the septa. I am not able to account for the difference in these septa as observed by Briquet and myself, except to suggest that his plants were grown under conditions which induced the sclerosis of the elements of the septa and which he has not described.

The most important additional fact concerning the structure of these organs, however, is that all of the specimens in the herbarium of the New York Botanical Garden, and of those cultivated by myself in the open, exhibit the pits or depressions mentioned above, and this feature is to be seen even in the first leaf of the seedlings. These pits seem to be the external openings of oil or resin glands which are situated immediately below each septum. The pit is partly closed by a chlorophylless outgrowth of the lower margin, which can be distinguished by the unaided eye as a minute scale. Goebel * describes similar outgrowths on the phyllodes of *Crantzia linearis*, an umbellifer of the same habit as *Oxypolis*, and despite the fact that they occur along one side of the leaf only, he holds the opinion that they are vestigial leaf-divisions. This conclusion can hardly be valid with respect to the pits and scales of *Oxypolis*. These formations are absent from the basal septa as they would be if vestigial leaf-divisions, but as a matter of fact the scales and pits originate on a line ninety degrees from the plane of the stipules. Furthermore the specialized structute of the formations in question militates against their acceptance as vestiges.

It was found that the floor of the pit is on a level with the plane of the diaphragm. It is this floor and the flap which closes the orifice only, whose structure indicates a specialization of function. With these exceptions the invagination is lined by a continuation of the normal epidermal cells of the phyllode, covered by a cuticle continuous with that on the outside of the leaf. The floor and flap have an epidermis of smaller cells the outer walls of which are slightly convex, forming small papillae. No cuticle is present. The small openings which occur in this epidermis measure about 19 μ in diameter and are formed by two cells broadly elliptical in shape. Directly below these epidermal cells and making up the greater part of the flap is a mass of irregularly shaped cells dovetailed compactly into each other. The epidermal cells as well as the cells of this tissue contain a great amount of resin or oil. Enlarged tracheae are to be found in great numbers leading into this compact tissue and forming a solid mass below it. The anastomosing bundles of the septa end here. In the light of this peculiar structure, it seems reasonable to regard these pits as glands for the secretion of oil or resin.

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* Goebel, K. Organographie der Pflanzen, 494. 1901.

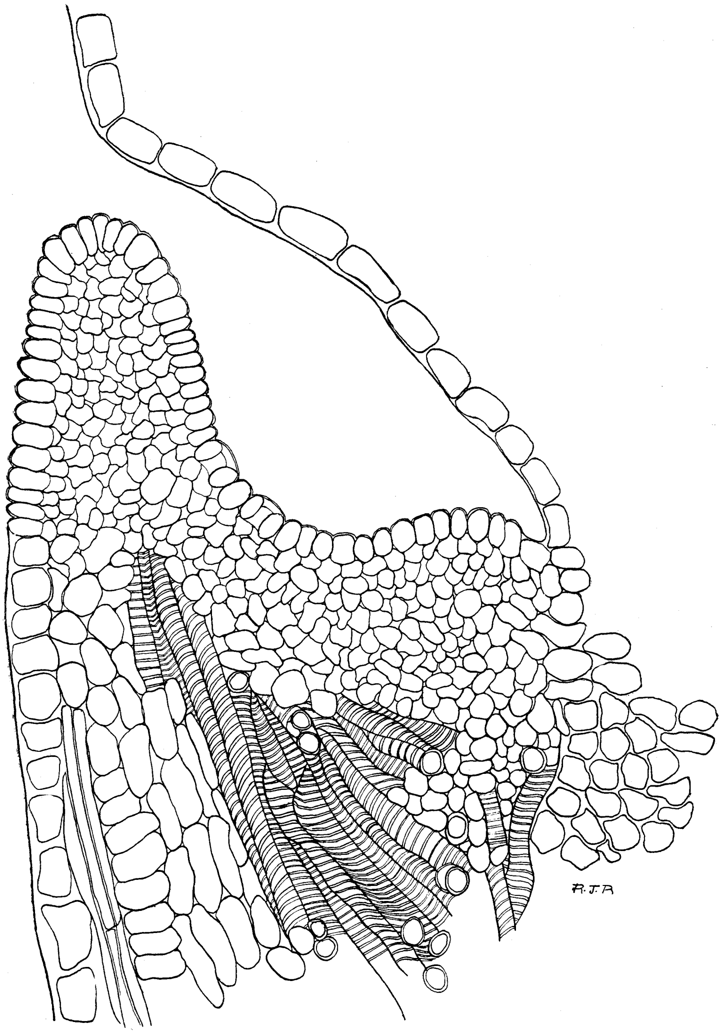

FIG. 1. Oil-gland of phyllode, × 140.

In opposition to Briquet, I am led to the conclusion that *Oxy-*

polis does not owe its peculiar structure to an adaptation to wet and dry periods, but that it is a true swamp or bog xerophyte in accordance with the generalization of Schimper, who supposes that the water of bogs and swamps contains such a large proportion of humic acid as to render absorption difficult. Plants growing in such places therefore have difficulty in securing a requisite supply, as if growing under arid conditions. Not all plants are capable of absorbing water from a mixture exhibiting a higher pressure than that of the cell-sap of the absorbing organs.

Dr. Shaw * has pointed out that the vegetation of a pond in its final stage is always xerophytic and has drawn attention to the fact that the continual deposit of organic material around the margin of a pond will produce a zone so much filled with humic acid as to be entirely devoid of vegetation. Dr. Cowles † has upheld this view of the xerophytic character of an undrained swamp and has frequently noted the remarkable assemblage of xerophytic adaptations such as leathery or hairy leaves and special structures for water absorption exhibited by the flora of peat bogs. In confirmation of this standpoint Dr. Cowles has pointed out that if plants growing in swamps of this type are xerophytic we ought to find them thrving in dry regions. And this he reports to be true; *Clethra alnifolia*, *Spiraea tomentosa* and *Myrica cerifera*, generally conceded swamp plants, have been found thriving and in all respects normal on dry hillsides.

As Briquet has indicated, the most superficial examination of the plant brings to light the unmistakably xerophytic character of the reduced leaf-surface and the strong development of hypoderm. On the other hand many of the characters which Briquet regards as demonstrating the hydrophytic nature of the plant, seem when viewed in the light of recent ecological work, to be adaptations either for water storage or the prevention of transpiration. The large thin-walled empty celled endoderm certainly exhibits capacity for water storage. The thick cuticle and the waxy incrustation of the epidermis, the accessory cells and the sunken position of the stomata, and the presence of resin glands all point to the conclusion that the conservation of water is the chief purpose met by the striking structural adaptations.

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*Shaw, C. H. The Development of Vegetation in the Morainal Depressions of the Vicinity of Wood's Hole. Bot. Gaz. 33 : 437. 1902.

† Cowles, H. C. Bot. Gaz. 27 : 293. 1899.

This view is strengthened by the experimental results. Two series of cultural tests were made. In one series a number of plants in pots of soil were enclosed in bell-jars and were thus grown in a saturated atmosphere. Others were entirely submerged in tanks of water. The phyllodes produced under these conditions were similar. In both cases these organs were delicate, hollow, terete, translucent, light green in color, and exhibited no trace of glands or pits. The stipules were membranous and reduced in width. The epidermal cells were without wax or cuticle and were greatly elongated longitudinally. The stomata were partly exserted and were of a reduced number, but retained their characteristic structure. In consequence of the regularity of the epidermal

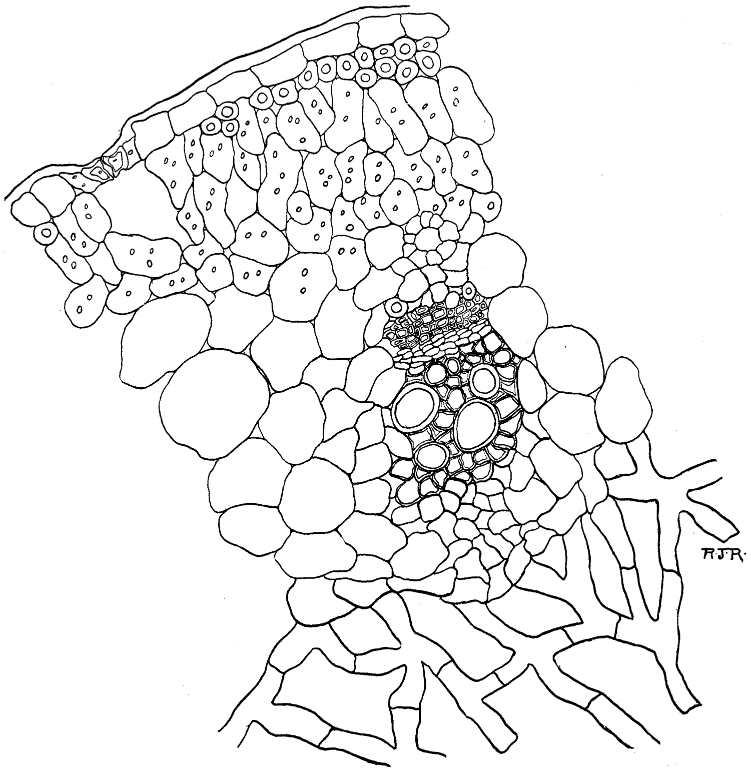

FIG. 2. Partial cross-section of phyllode, xerophytic form, × 140.

rows of cells, the stomata occurred in definite rows separated from each other by five sterile epidermal rows. Hypoderm was absent. The chlorophyl-cells followed directly upon the epidermis. This tissue was reduced to about three rows, and the palisade character of the first row of cells was not very marked. The endoderm was also less developed. It consisted of only one to three rows of cells. The stellate tissue of the other form was entirely absent here. As a consequence of the meager development of endoderm the fibro-vascular bundles jutted out into the central cavity. The xylem in the bundles was reduced and the position of the resin duct changed. In the normal type it was always to be found outside of the phloëm; in these phyllodes it was on the other side of the bundle near the xylem. This position of the duct has been pointed out by Van Tieghem as more primitive or juvenile. The diaphragms were composed entirely of thin-walled cells and the anastomosing bundles contained in them were much weaker and, contrary to the habit in the solid phyllode, anastomosed as freely at the center of the septum as about the edge. No trace of glands in the phyllode have been found and there is consequently no general convergence of bundles toward any single point in the margin.

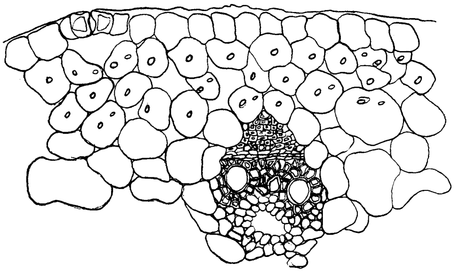

FIG. 3. Partial cross-section of phyllode, hydrophytic form, × 140.

The phyllodes of the submerged plants possessed in all cases the same structure as those grown under the bell-jar and exhibited an additional modification in their method of propagation. New plants were developed from the nodes of the xerophytic stems which had been developed before the plants were submerged and also in turn from the nodes of plants produced under water.

The water in which the immersed plants were grown presented none of the difficulties of absorption of the liquid in bogs. These submerged individuals as well as those in the bell-jars were seen to undergo true aquatic adaptations consisting in the loss of hypoderm of the central stellate tissue and of the glands; the reduction of the chlorophyl-bearing elements, of the endoderm, and of the number of stomata as well as of the xylem; the change in the position of the resin duct; the modification of the epidermal cells, stomata, cells of the septa and the course of the bundles through the septa; and the adoption of a new method of propagation.

These changes may be divided naturally into two classes, those which involve a suppression of xerophytic characters and those which are a means of adaptation to moist conditions and therefore hydrophytic in their nature. In the first class we must consider the loss of hypoderm and glands, the reduction of palisade-cells and water-storage tissue of the endoderm and the loss of cuticle; while we find in the modification of the epidermal cells, the reduction and modification of the stomata and the adoption of a new method of propagation types of structure peculiarly distinctive of hydrophytes. If the action of water free from high concentration of osmotic substances will induce such sweeping departures from the normal, it seems but reasonable to conclude that the plant is naturally a swamp xerophyte.

The adaptations described seem to have been most thoroughly adopted by the species since the characteristic structure of the phyllodes is to be found in the seedlings. These seedlings were raised from seed developed by the plants with which the experiments were made. The cotyledons were flat and linear in shape and 5 to 6 cm. in length. When the first leaf developed it exhibited the typical awl-shaped, septate character and bore glands and the accompanying scales along one side throughout its length. In internal structure it also resembled the later leaves in all respects, except that the hypoderm was absent and that the cells of the endoderm bore chlorophyl.

The chief results of importance brought out in the foregoing paper may be briefly summarized as follows:

1. The leaf-structures of *Oxypolis filiformis* are terete, awl-pointed phyllodes with numerous septa or diaphragms, and this form is exhibited even by the first leaf of the seedling. The

structure of the septa as examined by myself differs notably from that described by Briquet.

2. The phyllodes normally bear numerous glands sunk in pits which are edged with a minute scale. These glands are on a line at 90° from the plane of the stipules and the attendant scales may not be considered as vestigial leaflet structures as suggested by Goebel as to the scales of *Crantzia*.

3. Plants of *Oxypolis filiformis* when grown in a saturated atmosphere or under the influence of normal soil-water (submerged) exhibits marked hydrophytic adaptations of the phyllode. The changes ensuing under such circumstances emphasize still further the xerophytic character of the phyllodes as indicated by their anatomical character, and reënforce the conclusion that this species should be regarded as a swamp xerophyte.